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Chapter 1 : The worldwide leaf economics spectrum. - FPrime

Bringing together leaf trait data spanning 2, species and sites we describe, for the first time at global scale, a universal spectrum of leaf economics consisting of key chemical.

Ian Wright articles The worldwide leaf economics spectrum Ian J. Reich2, Mark Westoby1, David D. Pyankov24, Catherine Roumet11, Sean C. Bringing together leaf trait data spanning 2, species and sites we describe, for the first time at global scale, a universal spectrum of leaf economics consisting of key chemical, structural and physiological properties. The spectrum runs from quick to slow return on investments of nutrients and dry mass in leaves, and operates largely independently of growth form, plant functional type or biome. Categories along the spectrum would, in general, describe leaf economic variation at the global scale better than plant functional types, because functional types overlap substantially in their leaf traits. Overall, modulation of leaf traits and trait relationships by climate is surprisingly modest, although some striking and significant patterns can be seen. Reliable quantification of the leaf economics spectrum and its interaction with climate will prove valuable for modelling nutrient fluxes and vegetation boundaries under changing land-use and climate. Green leaves are fundamental for the functioning of terrestrial and the vegetation of different biomes is a major goal for plant ecosystems. Their pigments are the predominant signal seen from ecology and crucial for modelling how nutrient fluxes and veg- space. Nitrogen uptake and carbon assimilation by plants and the etation boundaries will shift with land-use and climate change. Animals, fungi and other heterotrophs in ecosystems are fuelled by photo- Data set and parameters synthate, and their habitats are structured by the stems on which We formed a global plant trait network Glopnet to quantify leaf leaves are deployed. The Glopnet data set nutrients in the construction of leaves, which in turn return a spans 2, species from families at sites approximately revenue stream of photosynthate over their lifetimes. The coverage of traits, synthate is used to acquire mineral nutrients, to support metabo- species and sites is at least tenfold greater than previous data lism and to re-invest in leaves, their supporting stems and other compilations4â€"11, extends to all vegetated continents, and represents plant parts. Mean annual temperature MAT ranges from These processes of investment and This covers most of the range of MATâ€"MAR space in which how these processes vary between species, plant functional types higher plants occur12 Fig. Here we report some global outcomes from our analyses. We focus on six key features of leaves that together capture many essentials of leaf economics. Species with high LMA have a thicker leaf blade or denser tissue, or both. Photosynthetic capacity is influenced both by stomatal conductance and by the drawdown of CO2 concentration inside the leaf carboxylation capacity. The photosyn- thetic machinery is responsible for drawdown of CO2 inside the leaf, a process also affected by leaf structure14, Phosphorus derives from weathering of soil minerals at a site, in contrast to nitrogen, much of which may be fixed from the atmosphere by plants. Long LL requires Figure 2 Three-way trait relationships among the six leaf traits with reference to LMA, one of the key traits in the leaf economics spectrum. The direction of the data cloud in three-dimensional space can be ascertained from the shadows projected on the floor and walls of the three-dimensional space. Results for necessarily a subset of those for each of the bivariate relationships. Biome boundaries are only approximate. Multi-dimensional analyses including from four to all can be expressed per leaf area, per leaf dry mass or per leaf volume. A six of the traits similarly showed the large majority of variation leaf-area basis reflects fluxes in relation to surfaces. It is a natural explained with a single axis Table 2. On a mass basis, leaf economics are quantified in variation is indicated by a loading or weight assigned to each trait. Scaling up to whole plants, mass-based can be thought of as a leaf economics spectrum. This spectrum runs expressions of leaf nutrient concentrations N mass, P mass , A mass from species with potential for quick returns on investments of and R mass are more tightly correlated than area-based expressions to nutrients and dry mass in leaves to species with a slower potential relative growth rates of seedlings or to absolute height growth rates rate of return. At the quick-return end are species with high leaf of young trees21, Here tion, short leaf lifetimes and low dry-mass investment per leaf area. We first quantify relationships among the six mass-based leaf Within growth forms or functional groups the principal axes of traits: We find that these variation had the same directionality of trait correlations as for the economic traits covary tightly across all species. Trait relationships total data set Table 2. Similarly, species grouped by major biome are similar for species pooled by growth form, plant functional type Fig. The concordance of these results is of special spectrum of leaf economic variation. Second, we treat photosyn- significance, indicating a coordination of these key leaf traits that is thetic capacity, R mass and leaf nutrient concentrations on a leaf-area consistent across major plant functional types, growth forms and basis. These relationships are not as strong as among mass-basis biomes. The amount of variation captured by the principal axis in traits, and we consider why. Third, we assess the influence of climate the different species groupings was also similar to that across all on leaf trait relationships. We find that, in general, the influence is species in most cases. Still, whereas different growth forms and Mass-based leaf traits functional groups were differentiated along the leaf economics The six mass-basis leaf traits varied by one to two orders of mag- spectrum when trait means were considered, the overlap between nitude across the data set. LMA ranged from 14 to 1, g m22 and species groups was large data not shown. Evergreen trees and LL from 0. A mass ranged from 5 to shrubs had longer mean LL and higher LMA than deciduous nmol g21 s21; dark respiration from 2. Con- extending to LLs almost as short as for the shortest-LL deciduous sidered pairwise, all leaf traits were highly correlated Table 1. Similarly, on average, shrubs and These correlations have been reported previously from smaller data trees had higher LMA and longer LLs but lower N mass, A mass and sets6â€"10, Here we have generalized the patterns over many more Rdmass than herbs and grasses, yet trees and shrubs spanned almost species, sites and vegetation types. N2- We moved beyond pairwise consideration of traits to determine fixing species had higher mean N mass than non N2-fixing plants, yet the extent to which leaf economic traits covary in multidimensional the range of N mass was larger and extended higher in non N2-fixing trait space. This covariation can be quantified as the proportion of species. In two-trait space, the principal axis is the Allometries among traits long axis of the ellipse resulting from two correlated traits. In multi- tionality of pairwise trait relationships. In variation through a hyperellipsoid A tenfold first principal axis in three-trait space Fig. Because some of the increase in P mass corresponded with a 4. P ratios decline as one moves minimum estimate of the dominance of this single spectrum in towards the end of the spectrum that represents quick returns on explaining variation across plant species worldwide. Further three- investments of carbon and nutrients. Coefficients of determination r 2 and sample sizes are given in the lower left section of the matrix. All relationships were highly significant, P , , 0. Further details allowing calculation of predictive regression equations for each pair of leaf traits are given in Supplementary Information. The principal axis or component explained LL and LMA were negatively correlated with this primary axis of variation while the other traits were positively correlated with it, both in the total data set and in data subsets defined by growth form or functional group. The same directionality of trait loadings and similarly high percentage of variance was explained by the principal axis with species grouped by site temperature, rainfall or altitude, or with sites grouped into major biome type following Fig. All data were logtransformed before analyses. C3, C4 indicate species with C3 and C4 photosynthetic pathways, respectively. The leaf economics and also because it relates to plant growth strategies and influences spectrum of species from low to high N mass also constitutes a plantâ€"herbivore interactions in food webs But a spectrum of leaf types in terms of N area tenfold greater dry mass invested per unit leaf area coincided with would be less informative. A given N area can result from low N mass fold longer LL. If LMA represents a species with long-lived leaves and low A mass, while this measure translated directly into fitness benefit, this might lead high N mass with low LMA represents the opposite. But wider variety of leaf types may be found at a given N area than at a continuing ecological success of low-LMA species shows that all else given N mass31â€" Here for example, LMA varied approximately is not equal. On average, a tenfold decrease in LMA, for example, fold at the grand mean of N area versus tenfold at the grand coincided with a fold increase in photosynthetic capacity. Further, low LMA, high A mass and generally faster turnover of Because of the covariation between leaf N and LMA, relationships plant parts permit a more flexible response to the spatial patchiness between leaf N and other traits changed substantially when of light and soil resources28, as well as conferring advantages via a expressed on an area rather than on a mass basis. As seen pre- compound interest effect, whereby carbon fixed earlier can be viously7â€"9,31,33, relationships between leaf N and A mass or dark reinvested in new leaves sooner27, On the other hand, high respiration were weaker when considered on an area basis, as were A mass requires high N mass, and the combination of high LMA and relationships between leaf P and other traits Table 3. By also high N mass may increase vulnerability to herbivory as well as including LMA in analyses, we can quantify the independent effects increasing energy losses via respiration9, which can be detrimental of leaf structure and nutrient content on A mass and dark respira- in situations where energy gain is low owing to low resource tion32, A mass increased with increasing N mass at any given LMA, availability, such as under low light conditions That is, both leaf structure and nitrogen concen- by highly varying LMA. The evidence contradicts this interpret- tration affect photosynthetic capacity5,6,8, The independent LMA ation. First, N area varied more widely than did N mass fold versus effect is most probably due to leaves with high mass per area having fold; data for 1, species. While a standardized major axis can still be fitted in such cases, its slope is essentially meaningless. All other relationships were highly significant, P , , 0. Further details allowing calculation of predictive regression equations for each pair of traits are given in the Supplementary Information. Worldwide, precipitation is correlated with based equivalent and had a different pattern of trait loadings. Once variation in MAT was controlled in a basis , and largely reflected a spectrum of increasing N area the trait multiple regression, LMA did indeed increase as rainfall decreased with the strongest trait loading; Supplementary Information. About half the residual variation was explained by a second Despite the substantial overlap in leaf traits of evergreen and principal axis, which expressed essentially the same trait corre- deciduous species, these species groups varied somewhat in their lations as the first axis from the mass-based analysis. Together, these leaf traitâ€”climate relationships. Area-based analyses for species grouped by growth 0. That is, LL of In summary, the coordination among leaf traits appears to be deciduous species was shorter at colder sites where the growing stronger and simpler on a mass basis than an area basis. This is not season was shorter. But in evergreen shrubs and trees, LL tended to because area-basis traits are less varied among species. This is consistent with concentrations and assimilation and respiration rates in a simpler cold climate vegetation being typically N-limited and demonstrat- way than on an area basis. Climate influence on leaf investment Trait coordination is largely independent of climate Plant ecologists have emphasized broad relationships between leaf A major aim of the Glopnet collaboration was to obtain enough traits and climate for at least a century. In particular, a general coverage of climate variation to dissect out effects of climate on tendency for species inhabiting arid and semi-arid regions to have relationships between leaf economic traits.

Chapter 2 : The worldwide leaf economics spectrum - CORE

Bringing together leaf trait data spanning 2, species and sites we describe, for the first time at global scale, a universal spectrum of leaf economics consisting of key chemical, structural and physiological properties.

Chapter 3 : The worldwide leaf economics spectrum

spectrum of leaf economics consisting of key chemical, structural and physiological properties. The spectrum runs from quick to slow return on investments of nutrients and dry mass in leaves, and operates largely independently of growth form, plant.

Chapter 4 : Fundamental tradeoffs generating the worldwide leaf economics spectrum

The worldwide leaf economic spectrum (WLES) is a strikingly consistent pattern of correlations among leaf traits. Although the WLES effectively summarizes variation in plant ecological strategies, little is known about its evolution.

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Rather, it is an extension of spectrum, with the same patterning of trait correlations seen the fact that so much of the *total variation in leaf traits is captured globally and in species grouped by growth form, biome or climate. by the primary axis of the leaf economics spectrum.*